Archaeocidaris whatleyensis sp. nov. (Echinoidea) from the Carboniferous Limestone of Somerset, and notes on echinoid phylogeny

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Synopsis

The new species *Archaeocidaris whatleyensis* is described from the Carboniferous Limestone of the eastern Mendip Hills of Somerset, England. The specimens came from the Clifton Down Limestone of Holkerian age, and their preservation suggests that they were buried rapidly.

The phylogenetic position of the species with respect to more advanced echinoids is discussed, using a cladistic approach. *Archaeocidaris* is seen as part of the stem group of all echinoids. *Miocidaris* probably includes stem echinoids, stem cidaroids and stem euechinoids; the echinothurioids are the primitive sister group to all other euechinoids.

Introduction

Field-work by R. Shaw in Whatley Quarry, Whatley, near Frome, Somerset (Nat. Grid ref. ST 727480) in April 1977 produced a well-preserved specimen of *Archaeocidaris* (E.76887; all specimens prefixed E are in the BM(NH), see p. 81. One of us (P.C.E.) revisited the quarry during the summer of 1977 and collected further specimens (E.76888, E.76889) from the same place in the quarry. A preliminary note on this material appeared in 1978 (Ensom 1978).

All the specimens came from fallen blocks of deeply weathered Carboniferous Limestone, found near each other. Specimen E.76887 was embedded in a calcareous silt; specimen E.76888 came from a silty calcilutite which contained the carbonized remains of small non-calcareous algae along bedding planes. The algae are identified as dasycladacean (? Chlorophyta; Elliott 1982 herein). Elliott makes a comparison with the fossil *Archaeobatophora* Nitecki (Ordovician) and *Inopinatella* Elliott (Silurian), and with the living shallow-water marine *Dasycladis* and *Batophora*: see p. 106.

This paper describes in detail the new species *Archaeocidaris whatleyensis* and discusses the phylogenetic position of *Archaeocidaris* with respect to more advanced echinoids.

Palaeozoic echinoids are rather rare, particularly those which are well preserved and nearly complete (Kier 1965). The holotype of the new species *A. whatleyensis* is especially well preserved, with many pedicellariae present, as well as the jaw apparatus and primary, secondary and miliary radioles. The paratype E.76887 displays features which are hidden or missing in the holotype. Perhaps the most interesting of these features are the remains of two compasses, comprising two outer portions and two inner portions. One of the most important features present on the holotype and on an isolated demipyramid (E.76899) is the very tuberculate nature of the demipyramid/epiphyseal suture faces. This tuberculation is present on *A. nerei* (BM(NH) 32846 and E.9328), and probably on other species of *Archaeocidaris*.

Bull. Br. Mus. nat. Hist. (Geol.) **36** (2): 77–104

Issued 28 October 1982

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1a

Fig. 1a   Apical surface of the holotype, E.76888.

The extensive work by Jackson (1912) described three species of *Archaeocidaris* in which the test is at all complete, *A. wortheni*, *A. rossica* and possibly *A. urii*. Unfortunately, Jackson did not describe the specimens in great detail.

Archaeocidaris is important to the phylogeny of more advanced echinoids. Euechinoids have features which are present in *Archaeocidaris* and which are usually regarded as advanced characters, such as hinge-joint lanterns, and foramina magna deeper and broader than the shallow foramina magna of cidarids. The lanterns of cidarids are socket-jointed, which is an advanced character.

Archaeocidaris is a stem echinoid. The classification used in the *Treatise* (Fell 1966) is mistaken to include *Archaeocidaris* with the Cidaroida. The taxon Perischoechinoidea is
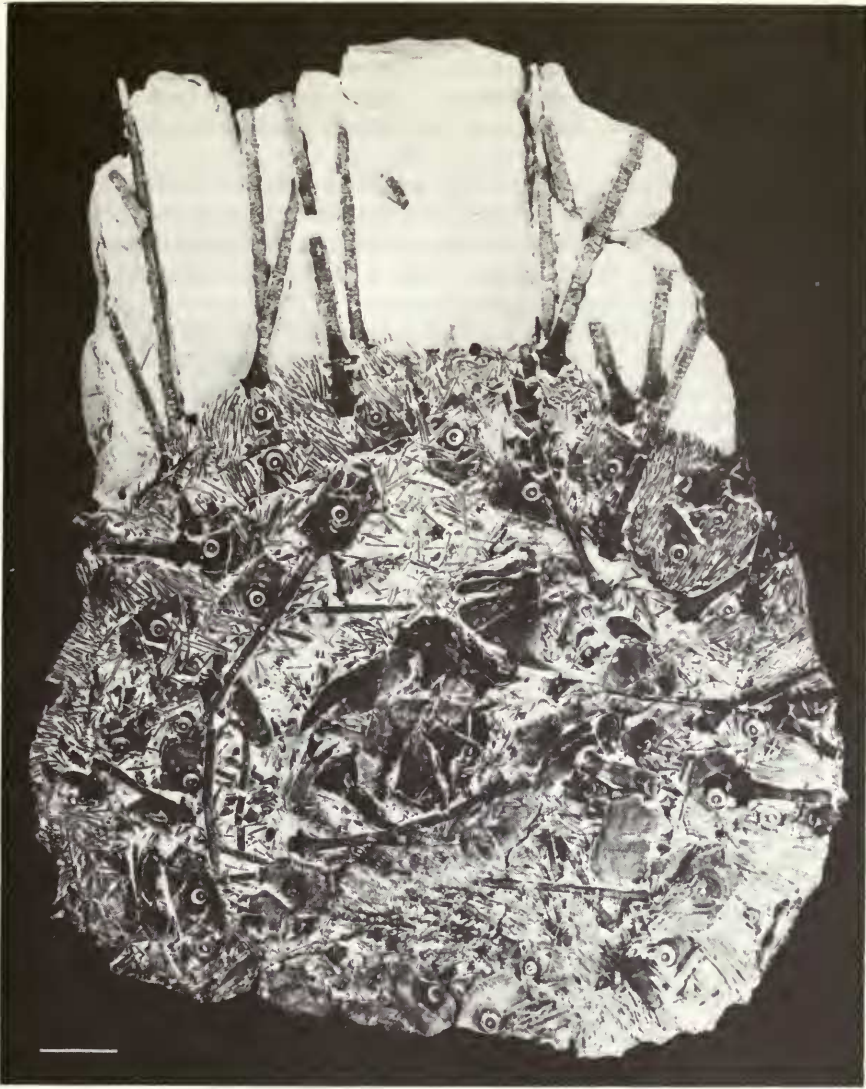
1b

Fig. 1b   Oral surface of the holotype, E.76888.

rejected as it is paraphyletic. Instead, the classification has to indicate the relationship by use of Hennigian terminology.

Preservation and stratigraphy

The tests of E.76887 and E.76888 were flattened after death. The additional apparently three-dimensional specimen E.76889 was recovered with the second specimen (E.76888) together with elements of other tests. We believe that E.76889 was flattened and then rolled up.

Trilobites collected from near where the echinoid specimens were found belong to the species *Linguaphillipsia matthewsi* (Hahn & Hahn) (identification by R. M. Owens, personal communication). *Linguaphillipsia* was first recorded in western Europe at Holwell Quarry, 3 km south of Whatley, on the southern limb of the Beacon Hill pericline (see Hahn & Hahn, 1973). Hahn & Hahn identify the horizon as low in the Clifton Down Limestone, Holkerian stage.

The echinoids were only partly exposed when recovered. Their development was facilitated by the relative softness of the matrix, which may be explained by a high proportion of silt in the limestone and the proximity of major solution features, including caves. Water appears to have been responsible for the partial decalcification or rotting of the limestone without affecting the specimens very much.

The exposed aboral surface of E.76888 was cleaned initially using a pin, brush and water. The exposed oral surface of E.76887 was cleaned initially by minimal use of an air-abrasive machine. The oral surface of E.76888 and the aboral surface of E.76887 required complete excavation from the matrix. Excess rock was removed from E.76887 with the aid of a diamond saw. The air-abrasive unit was then used on both specimens to reveal the remarkable detail.

Mode of preservation

The fact that two of the tests remained largely intact after death demands consideration.

Echinoids with rigidly sutured tests have a greatly increased chance of preservation in the fossil record over those with flexible tests, such as *Archaeocidaris*, which are more likely to disintegrate after death. The apical surface of E.76888 suffered little disarticulation; the primary and secondary radioles and pedicellariae have been flattened against the test, but their proximal ends remain close to their tubercles. The Aristotle's lantern remains, somewhat dissociated, in a central position. Most of the primary radioles are in contact with or lie near their corresponding tubercles. Secondary radioles are present on most plates though often displaced. A perignathic girdle is not present and never existed; however, peristomial plates are present. Unfortunately, no sedimentological information was present to indicate which way up the specimen had been buried.

The primary radioles on the adapical surface of the holotype have an approximately radial orientation, with a slight bias towards ambulacrum III or interambulacrum 3. On the adoral surface the orientation is mostly radial but the radioles at the ambulacrum III end of the test point outwards from it, almost parallel to each other. The secondary radioles are almost *in situ*, laid flat.

Most of the tips of the secondary radioles point towards interambulacra 3, 4 and 5. In interambulacra 2 and 3 some of the tips point towards the anterior ambitus. A further exception is in ambulacrum III where the shafts are parallel to the perradial suture. The adoral surface has been disrupted. This, together with the perfect preservation of the apical surface, suggests that the specimen was turned over, perhaps by a sudden influx of sediment which also suffocated the animal. The preservation of the delicate algal remains seems to confirm a rapid rate of sedimentation. The peristomial plates and the lantern collapsed into the body cavity, and minor disruption of the coronal system of the oral surface also occurred before burial of the test was complete.

The test of E.76887 is skewed. Primary radioles are almost completely absent, and secondary radioles are comparatively few. Secondary radioles are almost completely absent on the oral surface, and most of them form a confused mat on the aboral surface, though even here a significant portion of the test lacks them. Four interambulacral plates within this area are damaged. Two of them have only scars to indicate that a mamelon was present, and a deep groove crosses one of these. There is no disarrangement of the plates. Perhaps this represents damage inflicted by a predator. The matrix from which the specimen was extracted has geopetals and small-scale sedimentary structures (cross-bedding) which show that the specimen was buried upside down. The layer in which it was buried rests on a

poorly-sorted, silty microbiosparite containing crinoid, coral and brachiopod-shell debris as a coarse component. The matrix surrounding the specimen is a calcareous terrigene which is fine-grained and streaky in appearance with some small-scale cross-bedding. This suggests that an influx of sediment-laden water may have been partly responsible for the preservation of this specimen, though lack of spines and some disarticulation indicates a time lapse between death and final burial. In acroechinoids the lantern is frequently missing, or is very fragmentary, despite the possession of a rigid test which enhances the chance of fossilization (Smith 1981). This indirectly confirms that the new archaeocidarids were buried rapidly.

In both specimens the presence of much silt in the matrix can be demonstrated by treating samples with hot and cold dilute hydrochloric acid. The matrix of E.76887 had so high a terrigene content that a cube of rock remained intact after the carbonate had been removed by the acid. George (1972), in his discussion of Carboniferous Limestone lithologies, mentions the occasional input of terrigenes which he relates to the influence of St George's Land to the north. The greatest influence of St George's Land is marked by the deposition of the sandstone units of the Forest of Dean area during the Arundinarian and Holkerian stages. Perhaps exceptional conditions caused mud from St George's Land to be deposited even so far south as Whatley.

Such exceptional conditions may have smothered laterally extensive colonies of *Lithostrotion* which are common on bedding planes within the Clifton Down Limestone (Green & Welch 1965); these corals are well exposed in the adjoining Lime Kiln Hill Quarry. These conditions would also account for the sudden death of the Archaeocidarids at Whatley Quarry. Similar events affected the Lower Avonian Limestones, killing crinoids *en masse* (George 1972 : 233).

Systematic description

Class **ECHINOIDEA** Leske, 1778

Family **ARCHAEOCIDARIDAE** M'Coy, 1844

Genus *ARCHAEOCIDARIS* M'Coy, 1844

Archaeocidaris whatleyensis sp. nov.
Figs 1–19[1]

DIAGNOSIS. The primary interambulacral radioles have an approximately triangular cross-section with a row of spinules along the two base edges of the triangle.

MATERIAL. There are three almost complete tests and sundry fragments from these, and fragments from other disintegrated tests. The **holotype** is E.76888 (Figs 1a, 1b, 3a, 3b), with two paratypes, E.76887 (Figs 2a, 2b, 5a, 5b) and E.76889 (Fig. 6). All the specimens are in the collections of the Department of Palaeontology, British Museum (Natural History).

The specimens are from the Lower Carboniferous, Dinantian, Holkerian Stage, Clifton Down Limestone, from Whatley Quarry, near Frome, Somerset (National Grid ref. approx. ST 727480). E.76888 and E.76889 were collected and presented by P. C. Ensom; E.76887 was collected and presented by R. P. Shaw.

SHAPE. All the specimens have been flattened dorsoventrally. The shape of the living animal is unknown, but was probably an oblate spheroid. The holotype, E.76888, is 107 mm across its broadest part, excluding radioles, and has a domed central area on the apical surface where the test has collapsed over the Aristotle's lantern. The paratype E.76887 is 82 mm across its widest part, and paratype E.76889 is 40 mm across its widest part. E.76889 is about 20 mm tall, but this is because the specimen had been rolled up. All specimens have suffered some plate displacement.

[1] Scale bar represents 10 mm, broken scale bar represents 5 mm.
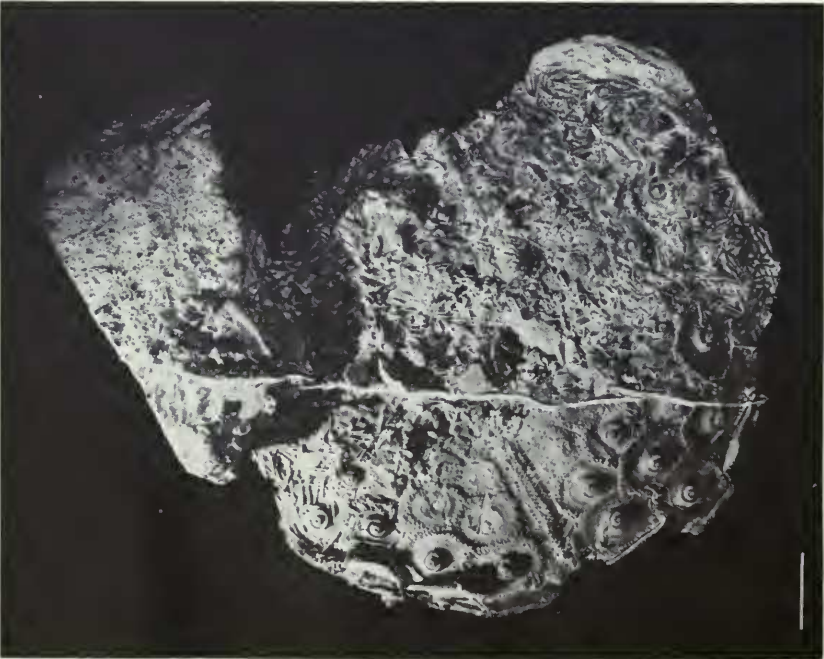
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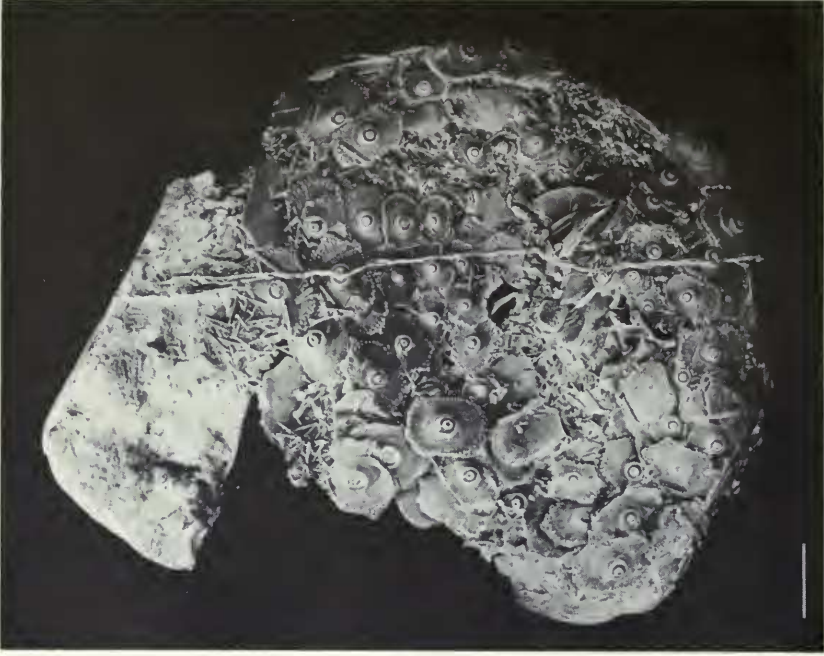
2 a

Fig. 2   Paratype E. 76887. a, apical surface. b, oral surface.

APICAL SYSTEM (1). Ocular plates. No plates on any of the specimens can be positively identified as ocular plates. The apical surface of the holotype is covered by secondary radioles. By following the course of the ambulacra adapically, the approximate positions of the ocular plates can be determined. Several small tubercles can be seen in this position, with small radioles lying scattered adjacent to the tubercles, as seen at ambulacrum III.

(2). Genital plates and madreporite (Figs 7, 8, 17a). The genital plates cannot be positively identified because of the disrupted state of the tests of the paratypes and the spine cover of the holotype. However, on paratype E.76887 there are two plates which are probably genital plates. One of these is present on interambulacrum 5, seen from the adapical surface, and is situated at the adapical end of the interambulacrum which it terminates (Fig. 7). Its margins are mostly obscured by other plates and test debris, but in position Va the margins can be seen. The transverse margin is curved so that it follows the adjacent edge of the interambulacral plate. Adoral to the curve there is a flange to imbricate with the inter-ambulacral plate. The lateral margin is convex and has no flange. The apical transverse margin is hidden by periproctal plate debris. The adradial margin is convexly curved the whole of its length. In the adoral position of the mid-line of the plate, there is a hole which may be the genital pore. It has an elliptical outline, with the long axis following the mid-line. Plate ornament consists of a few randomly distributed small tubercles. One of these is present on the adoral margin of the genital pore, growing into the pore. The plate is 5 mm long.

The second probable genital plate is present on the oral side of the specimen in inter-ambulacrum 1, with the inner surface of the plate visible. The shape is rather like a square with one corner removed leaving a third of one side of the square and two-thirds of another. The genital pore is circular and is situated near the margin of the side of the square nearest the mouth. The plate has a smooth surface and is 4·5 mm long.

The madreporite is present on the holotype (Fig. 8) and on paratype E.76887. It appears to be *in situ* on the holotype, but as most of it is masked by small radioles, we cannot be sure. On the paratype it is present on the apical surface, and is not *in situ*, but still remains in interambulacrum 2. It is about 6 mm long and about 4·5 mm wide. The narrower ends are obscured by test debris. The plate appears to be bilaterally symmetrical about the greater dimension. The margin has a flange around it which is interrupted in at least four places. The plate above and within the flange is convex and has several small tubercles randomly distributed, and many tiny pores over the whole of the surface. On the madreporite of the holotype the tubercles bear small radioles.

(3). Periproct. This is not visible on the holotype nor on the paratypes. However, on paratype E.76887 there are several small plates on the apical surface which are probably periproctal plates. They each are irregular in outline and have ornament consisting of tubercles arranged in a regular, concentric fashion on some of the plates. On the holotype the area occupied by the periproct is covered by small radioles, indicating that the tubercles on the paratype E.76887 also bore radioles.

AMBULACRA (Figs 7, 10, 20b, 21). The ambulacra are faintly sinuous, almost straight. Each ambulacrum consists of two rows of simple plates with no suggestion of compounding. The paratype E.76887 shows ambulacrum I extremely well from the apical surface. It is about 5 mm wide, from the adapical end to the ambitus where it is totally disrupted. The width of the interambulacrum at the ambitus is 40 mm, so that the width ratio of ambulacrum to interambulacrum is 1 : 8 at the ambitus. This ratio alters towards the apical system where the ambulacral width remains the same but the interambulacral width decreases. Each ambulacral plate is wide and low. The pore pairs as seen from the outer surface are almost centrally placed, slightly perradial. The pores of a pair are unequal. The perradial pore has an elliptical outline while the adradial pore is comma-shaped and larger. Both pores have their long axes parallel to the width of the plate. Each pore is surrounded by a slightly raised wall which joins between them and forms an adorally pointing projection. Adapical and adoral to the projection is a long, low, triangular pit. The inner walls of each pore are steep and smooth and are parallel to the radius of curvature at each pore.

The ornament of the outer surface of each ambulacral plate consists of between three and five small tubercles. The plates with three tubercles are found near the apical system; those with five are found where the ambulacral plate expands adradially into the V-shaped junction on the adradial margins between two adjacent interambulacral plates.

All the ambulacral plates have two tubercles on their perradial parts – one central marginal tubercle and one inner tubercle close to the adoral perradial suture. This suture sometimes truncates the inner tubercle.

The ambulacral plates imbricate adorally by means of flanges and bevels, and steeply sloping adoral and adapical margins (Figs 20b (p. 94), 21 (p. 95)). Each plate has a broad, approximately triangular flange on the adapical-adradial end. The flange tapers perradially to disappear by the adradial pore. The flange is expanded on some plates adradially at the V-shaped junction between two interambulacral plates. The flange reappears by the central projection and expands adapically and perradially to a level with the adapical part of the inner tubercle. On the underside of each plate there is a corresponding bevelling on the opposite side to the flange, so that each ambulacral column can imbricate. The adoral margin of an adapical plate imbricates over the adapical margin of its adoral neighbour and the adoral perradial margin of one plate imbricates over the adapical perradial margin of its adjacent neighbour. The interambulacral plates are able to imbricate perradially over the ambulacral plates.

INTERAMBULACRA (Figs 7, 9, 12, 15a, 15b, 20a (p. 94), 22 (p. 97)). There are four columns of plates to each interambulacrum. Most plates bear a single, large, perforate tubercle, surrounded by scrobicular tubercles.

The arrangement of the interambulacra is best seen in specimen E.76887, where the spines have been lost, and the columns on both the adapical and adoral surfaces are clearly visible. The interambulacra of the holotype are obscured by small spines over the adapical surface and are disrupted on the adoral surface. Description of the interambulacra is therefore based on the paratype E.76887, on interambulacra 1 and 5 of the adapical surface, and 1–4 of the adoral surface.

The interambulacral plates are wider than tall, larger at the ambitus, and decrease in size adapically and adorally. The plates on the adoral surface all bear large primary tubercles, but the plates of the adapical surface (see Fig. 7) have no large primary tubercles on the first two horizontal series. The plates without large primary tubercles have central swellings with widely spaced concentric scrobicular tubercles over the remaining plate. The plates with large primary tubercles have scrobicular tubercles also.

Each primary tubercle (see Fig. 12) is in the centre of the plate. It has a very low basal terrace with a broad oval outline. The circular, gently concave boss rises steeply and is slightly tilted, with the shallower slope on the adoral face. At the top is a high, thick parapet. The platform is flat and about the same width as the parapet rim. Some plates have a slight excavation on the adoral and adapical sides. The mamelons have straight necks, and are either hemispherical, or cylindrical nearer the peristome. The foramen in either case is deep and has either a circular or a D-shaped (or sometimes kidney-shaped) outline. Where the foramen is D-shaped and the platform deep it is likely that the radioles moved mainly parallel to the long axis of the foramen. The plates of the two inner interambulacral columns are hexagonal and the plates of the outer two columns are pentagonal, with the adradial margin more or less convexly curved (Fig. 7).

Secondary tubercles are present on all interambulacral plates. Details of structure have been lost owing to slight abrasion or decalcification of the test. However, it shows the small tubercles each to have a convex boss, no parapet and a rounded imperforate mamelon arising from the boss. There is one complete ring of tubercles around the scrobicule of each primary tubercle. At the adradial and interradial ends the plate develops further rows of tubercles which would form up to four rings of tubercles if the plate was wide enough. Radiating from the basal terrace across the scrobicule are weak plications. Each plication has at its proximal end a secondary tubercle of the first ring. The subsequent incomplete rings of tubercles may

Fig. 3   Stereo-photographs of the holotype, E.76888. a, apical surface. b, oral surface.
Fig. 4   Primary radioles of the holotype, E.76888, showing spinules and crushed distal ends.

alternate behind the first or may be situated directly behind the first – there is no constancy in this arrangement.

The secondary tubercles protrude over the plate margin to give a scalloped appearance to the plate. This is especially noticeable on the adoral surface of paratype E.76887. The tubercles of one plate interlock with those of its neighbours (Fig. 9). The adradial plate margins of the two outer columns of interambulacral plates interlock with the adradial margins of the adjacent ambulacral plates.

Along the adoral margin of each interambulacral plate there is a flange which continues around the adoral interradial margin (Figs 12, 20a, 22). The outer columns of plates have flanges on the adapical interradial margins, but the inner two columns of plates do not (Fig. 12). The facet on the internal surface at the edge of the adradial margin of each outer plate is smooth and concave and imbricates over the adjacent ambulacral plates. The adoral adradial and adapical adradial margins of the inner columns of plates have narrow facets and shallow grooves undercutting the tubercles of the plate margins. The adapical margins of the outer and inner columns have similar facets and grooves. This arrangement allowed the plates, in life, to flex slightly about the contacts as a hinge. On contraction of the assumed meridional muscles, the curvature of the test would be increased, by one margin rotating over an adjacent margin. Measurements for a typical interambulacral plate from near the ambitus of the holotype and paratype E. 76887 are:

	Holotype E.76888	Paratype E.76887
Width (parallel to horizontal sutures)	13·0 mm	11·0 mm
Height (perpendicular to horizontal sutures)	9·2 mm	7·0 mm
Height of tubercle (scrobicule to mamelon)	2·0 mm	1·8 mm
Diameter of mamelon	1·5 mm	0·9 mm
Maximum length of foramen	0·5 mm	0·2 mm

The holotype has at least seven plates per column, some obscured by spines. The paratype E.76887 has at least nine plates per column.

Certain interambulacral plates of the holotype are slightly unusual. One such plate is present on the adoral surface at interambulacrum 1 (Fig. 15a). It has secondary tubercles on the surface of the scrobicule, and four or five on the basal terrace and lower boss. The boss has steep, convex sides. On the top of the adoral side are two small tubercles in shallow hollows. In the centre of the boss is a trilobed perforate mamelon with a platform aboral to it. The plate is 10 mm wide and about 5·5 mm tall.

Other unusual plates are seen on the adapical surface of the holotype and are the first ones of the interambulacral columns to bear tubercles. They can be seen in interambulacra 4 and 5. The plate in interambulacrum 4 is mostly covered by secondary radioles but the primary tubercle is exposed. It has no basal terrace, the boss is low and convex and the mamelon arises directly from the boss. The mamelon is very elongate – 1·3 mm long, 0·5 mm wide – and forms a thin wall around a correspondingly elongate foramen. The wall rises gently to a sharp edge in the middle of the longer sides. There are two primary radioles lying very close by, almost in contact with the mamelon. They probably belong to the tubercle (Fig. 15b).

There is a variation in the distribution of tubercles with D-shaped foramina between the holotype and the paratype E.76887. The latter has the first five or so tubercles, from the apical surface to the ambitus, with D-shaped foramina. The long axis of the D is parallel to the ambitus. The remainder of the tubercles have circular foramina. The holotype has circular or just oval foramina from the apical surface to the ambitus. Adoral tubercles have circular foramina. Paratype E.76889 also has D-shaped and circular foramina.

PERISTOME AND ARISTOTLE'S LANTERN (Figs 16a–d, 17b, 18a–b, 19a–c). None of the specimens has the entire peristome preserved. However, the holotype and paratype E.76887 have most of the lantern present. The holotype has some peristomial plates. Other fragments of lantern – E.76899 (Figs 18a–b), E.76900 (Figs 19a–c) – come from other specimens of the
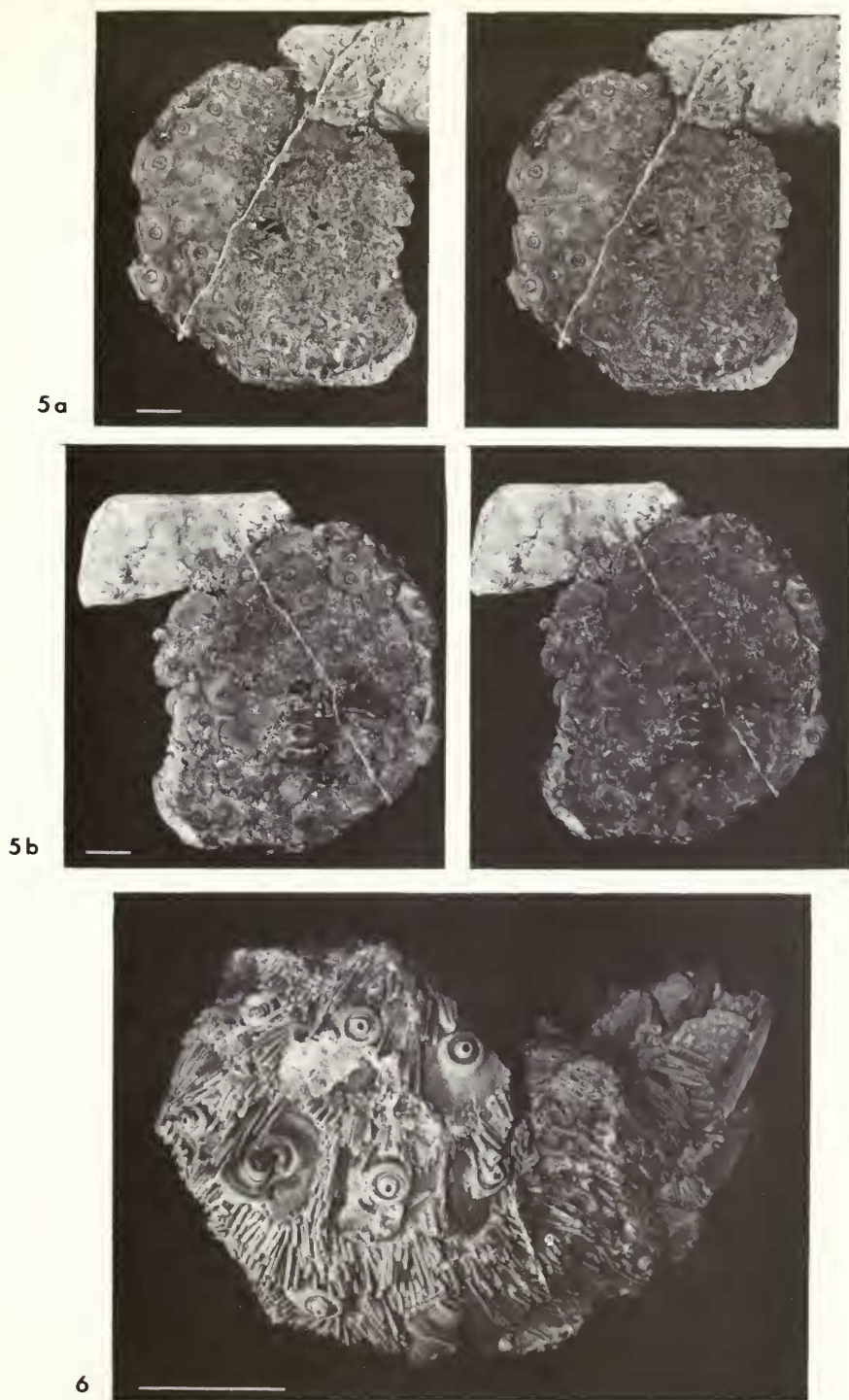
Fig. 5   Stereo-photographs of paratype E.76887. a, apical surface, b, oral surface.

Fig. 6   Paratype E.76889.

same species from the same locality and serve to clarify the morphology of the lanterns of the more complete specimens.

(1). Peristome border. Only one plate on paratype E.76887 probably came from the peristome border. This plate is present within the area of interambulacrum 5 on the oral side. It has basically the same structure as the other interambulacral plates, with a tall cylindrical mamelon with circular foramen. It differs from other plates in having one horizontal margin truncated as far as the basal terrace, probably by resorbtion at the edge of the peristome. There is no indication of apophyses or other muscle attachment points for the control of the lantern.

(2). Peristomial plates (Fig. 16d). These are scattered over the adoral surface of the holotype, and in the area around interambulacrum 3 there are seven ambulacral peristomial plates lying close together and imbricated with each other. Each ambulacral peristomial plate consists of a long, curved, projecting part, with a large expanded blade at one end and a small blade at the other. The expanded blade is adradial, the smaller blade perradial. There are two shallow pits adoral to the part where the projection joins the expanded blade. By comparison with living echinothurioids (see Sarasin & Sarasin 1887–93) the adradial expanded blade probably served for the attachment of peristomial muscles. The outer surface has a row of tubercles along the adoral edge. These bear small spines, some of which remain almost in life position.

The peristomial plates imbricate orally. When seen from the outside, the oral edge of a plate overlaps the aboral edge of its oral neighbour. Interradial peristomial plates are less readily recognized, but are probably represented by several irregularly-shaped plates on the adoral surface of the holotype, with smooth inner surfaces and with tubercles on the outer surface. These plates are much smaller than the ambulacral peristomial plates. Typical measurements for one of each are:

ambulacral peristomial plate	{length of expanded blade-shaped part	2·7 mm}	5·2 mm
	{length of projection	2·5 mm}	
interradial peristomial plate length		1·5 mm	

(3). Aristotle's lantern (Fig. 16a). a, Demipyramids. There are thirteen demipyramids visible on the adoral surface of the holotype, the three extra ones being due to the inclusion of fragments of the test of another individual of the species. Six demipyramids are visible on the adoral surface of the paratype E.76887.

An isolated demipyramid, E.76899 (Fig. 18a, 18b), belongs to neither E.76888 nor E.76887. The holotype has two pairs of demipyramids juxtaposed to form two complete pyramids, seen in interambulacra 3 and 4. The other demipyramids lie scattered nearby. All the demipyramids of the paratype E.76887 are scattered over the adoral test.

Each demipyramid is wide (pyramidal suture to wing edge), deep (outside to inside) and short (top to bottom). Each has a wide and fairly deep foramen magnum, with a shallow-angled concave side. The retractor muscle scar is a deep groove, broad and V-shaped. The deepest part of the groove is about halfway along the length of the demipyramid, shallowing towards the upper surface of the demipyramid. The angle of the scar is 30°.

Fig. 7   Part of paratype E.76887 showing the imbrication of the ambulacra, the overlapping of displaced interambulacral plates. The genital plate (g), secondary radioles, D-shaped foramina of the interambulacral primary tubercles and the inner portion of a compass (ic) are also shown. The plates at the ambitus show facets on the adapical margins of interambulacral plates, and on the surface of interambulacral plates there are radial striations.

Fig. 8   The madreporite of the holotype, E.76888, mostly hidden by secondary radioles.

Fig. 9   Interambulacral plates of E.76887 showing the interlocking of secondary tubercles. Radial striations on the plate surface are visible.

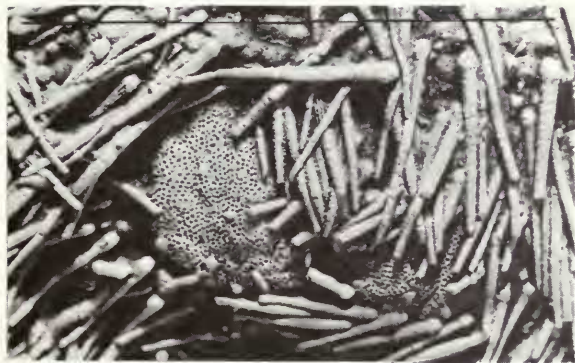Fig. 10   Part of an ambulacrum of the holotype, seen from the inner surface of the test.

Fig. 11   Base of a primary radiole of paratype E.76889 showing an infilled centre.

Fig. 12   An interambulacral plate from E.76887 showing two adoral flanges (af).
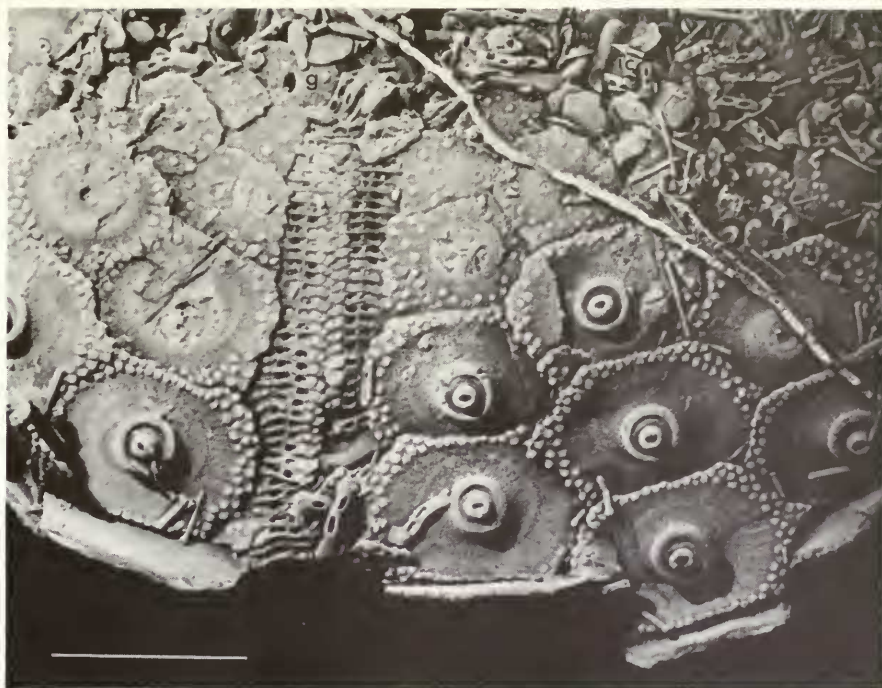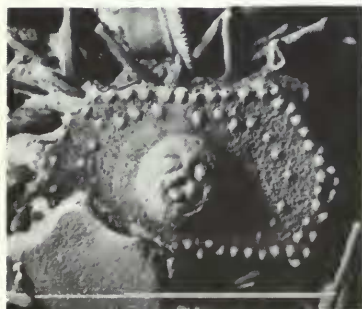
The edge of the wing is gently, convexly curved to a level just below the deepest part of the retractor muscle scar. The edge then steepens its angle to almost vertical down to the tip of the demipyramid. The edge of the wing forms a thin wall for the retractor muscle scar, from the epiphyseal suture to the start of the nearly vertical part.

The surface of the wing has many curved ridges for interpyramidal muscles. They extend from the outer edge of the wing to the innermost edge where they give rise to faint serrations. The ridges are curved, being concave towards the epiphysis. The wing is almost triangular in outline, with an irregular epiphyseal suture, a convex outer edge to the wing, and a convex inner edge which meets the dental slide at right angles. The inner edge of the wing is here produced into a flange as part of the slide, and continues to the top of the demipyramid. The angle between the wing and the outside of the demipyramid is about 70°.

Close to the pyramidal suture there is a thin groove from the foramen magnum to the bottom of the demipyramid. Farther away from the suture is a broad, parallel-sided, gently convex portion, which also forms the other wall of the retractor muscle scar. The outermost tip of the demipyramid is straight. The inner surface of the demipyramid is concave across the width and down the length. The dental slide is a smooth, parallel-sided structure, raised above the area adjacent to the pyramidal suture. The lower end of the slide is straight, and the upper end sharply curved and undercut, and does not reach the margin of the foramen magnum. The area adjacent to the pyramidal suture tapers very gently from the foramen magnum to the top of the demipyramid. It is smooth, and partly represented on the outside of the demipyramid by the raised portion running from the foramen magnum to the tip. The remainder of the inner surface of the demipyramid is broad and tapers towards the prong.

The top surface of the demipyramid is sutured to the epiphysis. The margin of the surface is smooth and narrow around the prong, but widens to about three times the width a short way from the inner margin along the interpyramidal side. The wider part also has several very small pits in its surface. There is a narrow shelf from the outer edge to the inner edge partly formed by the smooth expansion of the margin and partly by a deeply pitted area. The vertical surface of the prong is heavily tuberculated and has several pits sunk vertically into the surface. The tuberculations are elongated and have vertical long axes.

b, Epiphyses (Fig. 17b). There are four epiphyses visible on the holotype, and three on paratype E.76887. The suture surface of the epiphysis with the demipyramid has heavy tuberculations which correspond to depressions in the surface of the demipyramid. The outer surface of each epiphysis is smooth. There is a flattened inner tubercle on the horizontal surface at the inner end of the epiphysis, and a bilobed, kidney-shaped outer tubercle directly behind it. On the interpyramidal surface of the epiphysis, extending from the outer margin to just over half way along the epiphysis, is a glenoid cavity. It is a concave, triangular depression, wider at the outer end, tapered beneath the bilobed tubercle.

c, Teeth (Fig. 16a, 16b). There are five teeth present on the holotype, two of which are almost *in situ* within the pyramids. There is only one tooth on paratype E.76887 and none on the rolled-up paratype E.76889. Each tooth is long and wide and is gently curved across the width (convex to the outside) and strongly curved along the length (convex to the outside) to fit the curvature of the dental slide.

The teeth are longitudinally striated and grooved. Down the middle of the outside of the

Fig. 13   Part of ambulacrum III of the holotype E.76888 close to the madreporite, showing secondary radioles, miliary radioles, and the smaller pedicellariae.

Fig. 14   Holotype E.76888. a, large pedicellariae amongst primary and secondary radioles of the adapical surface. b, small pedicellariae, miliary and secondary radioles, along ambulacrum III. The tubercles and stems of the pedicellariae can be seen lying close together.

Fig. 15   Holotype E.76888. a, unusual adoral interambulacral plate, showing a trilobed mamelon. b, unusual adapical interambulacral plate with two primary radioles.

Fig. 16   Holotype E.76888. a, the broken Aristotle's lantern, showing demipyramids, epiphyses, rotulae, and teeth. Also present are several peristomial plates. b, detail of a, showing teeth with serrated tips.

17a

16c

17b

18a

18b

16d

19a

19b
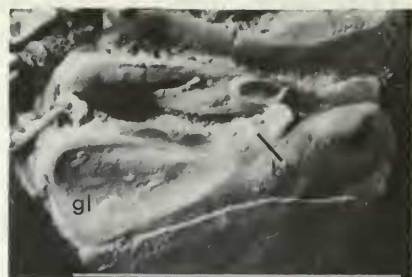
19c

tooth is a broad double ridge corresponding to the smooth areas adjacent to the inter-pyramidal sutures on the insides of the demipyramids. The dental slide corresponds to the grooved portions on either side of the central double-ridged part of the tooth.

The tip of each tooth is serrated, with a single large median serration, and three smaller serrations either side of it. Each point of each serration is in a direct line with a groove on the tooth. The sides of the median serration overlap the proximal ends of one and a half of the lateral serrations each side of the tooth. If the serrations are ignored, a semicircular outline would be formed and not a half ellipse or a V shape.

The innermost ends of the teeth are not visible in the specimens as they are hidden by fragments of the test.

d, Rotulae (Figs 16a, 19a–c). There are three rotulae visible in the holotype, one in paratype E.76887, and a complete isolated rotula, E.76900 (Figs 19a–c). Only one rotula is close to its normal position, and this is in interambulacrum 3 of the holotype (see Fig. 16a), lying next to a jaw. Other rotulae have been completely separated from their jaws.

The rotulae of the specimens are the same length as the epiphyses. Each one is a sturdy, bilaterally symmetrical structure. The single isolated rotula (E.76900) is 9·9 mm long and 2·5 mm at its widest point, a ratio of almost 4 : 1. The upper surface is smooth, narrow towards the outer end at the epicondyles, wide from the centre to the inner end. The outer end is bilobed, forming condyles which articulate with the glenoid cavity. The inner end has a thick semicircular wall around a deep conical pit, open at the innermost end. The wall has a steep, deep, narrow groove from the top of the wall to the depth of the pit.

On the lower surface, the condyles taper beneath the upper surface, and also towards the two-part median fossa. There is a deep groove either side of the rotula, extending from the epicondyle of each condyle to the median fossae. The median fossa of each side has a large triangular facet and a smaller triangular facet separated from each other by a low ridge. The outer part of the two-part fossa has a raised rim at the outermost end.

The inner fossa of each side is situated on a downwards-pointing projection of the innermost end of the rotula. It takes the shape of a quarter circle. At the uppermost edge, a very low ridge separates the inner fossa from the interior rotula muscle scar, which is elongate from the edge of the inner end to a position just beneath the semicircular wall of the upper surface.

The sides of the rotula, apart from the condyles, slope towards the centre of the underside and join in a short flat ridge from the inner end of the condyle to the innermost end of the rotula. The external rotular muscle scar is present on the side of the rotula, at the outer end of the median fossa.

e, Compasses. There are four fragments of compass present in paratype E.76887 – two inner portions and two outer portions (Fig. 17a, 17b).

Each inner portion has a triangular cross-section and a hooked inner end. The upper

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Fig. 16 Holotype E.76888. c, epiphysis and rotula. The epiphysis is still *in situ* on its demipyramid, and shows the glenoid cavity (gl) and the bilobed tubercle (bt). d, the peristomial plates.

Fig. 17 Paratype E.76887. a, the outer portion of a compass (oc) showing the two long spikes and short lateral spikes. The madreporite (m) and an inner portion of compass (ic) are also visible. b, part of the inner contact surface of an epiphysis, showing the tuberculation. Also visible is the demipyramid belonging to the epiphysis and part of another epiphysis. A part of an inner portion of a compass is visible just to the right of the tuberculate epiphysis, and shows the triangular pit in its end.

Fig. 18 Demipyramid E.76899. a, the inner surface showing the dental slide. b, the upper surface showing the heavily tuberculated and deep-pitted demipyramid–epiphyseal contact surface.

Fig. 19 Rotula E.76900. a, upper surface. b, lower surface. c, side view. Abbreviations: cond = condyle; epicond = epicondyle; fo.i = inner fossa; fo.m = median fossa; m.ro.e = exterior rotula muscle-scar; ve = vestigial; m.ro.i = interior rotula muscle-scar. (Terminology of Märkel, 1979.)

surface is narrow, and slopes steeply over the sides, then curves beneath to form the triangle. The hook is down-curved from the upper surface and ends in a sharp point. On its lower surface there are two facets which meet in the centre in a blade. The non-hooked end is broader, and has a shallow triangular pit in its cross section. One of the inner portions appears to be complete (Fig. 17a). It has its hooked end on the adapical surface, and its broad end on the adoral surface, having been forced through the test *post mortem*. The other inner portion, on the adapical surface, is slightly damaged on its broad end.

The outer portion of the compass has a triangular cross-section on its inner end, with a shallow triangular pit, similar to the pit in the end of the inner portion of the compass (Fig. 17a). The triangular part flattens out towards the centre of the length of the outer portion. Two short lateral spikes are present, pointing towards, and form the attachments for the intercompass muscles. Farther towards the outermost end there are two long, thin, curved prongs. The triangular part of the outer compass is straight, but at the flattened area the portion begins to curve downwards and becomes steeper along the prongs. The angle between the prongs is about 70°, but because of its position within the test, it is not possible to measure this angle accurately. The length of the outer part of the compass without the prongs is 5 mm; length of the prongs is 4 mm. The length of the inner part of the compass is 3·6 mm. There is one complete outer portion of a compass and one incomplete portion which has lost its prongs.

RADIOLES (Figs 4, 6, 8, 11, 13, 14b). (1). Primary interambulacral radioles (Fig. 4). These are long and slender. Each radiole is approximately triangular in cross-section for most of its length, with convexly curved sides. Nearer to the milled ring the section is circular. Along the length of the shaft there are two rows of spinules, one row at each angle of the base of the triangle.

The holotype has several primary radioles which are in close contact with their tubercles. The lateral spinules are present on the adoral surface of the radiole and point towards the tip
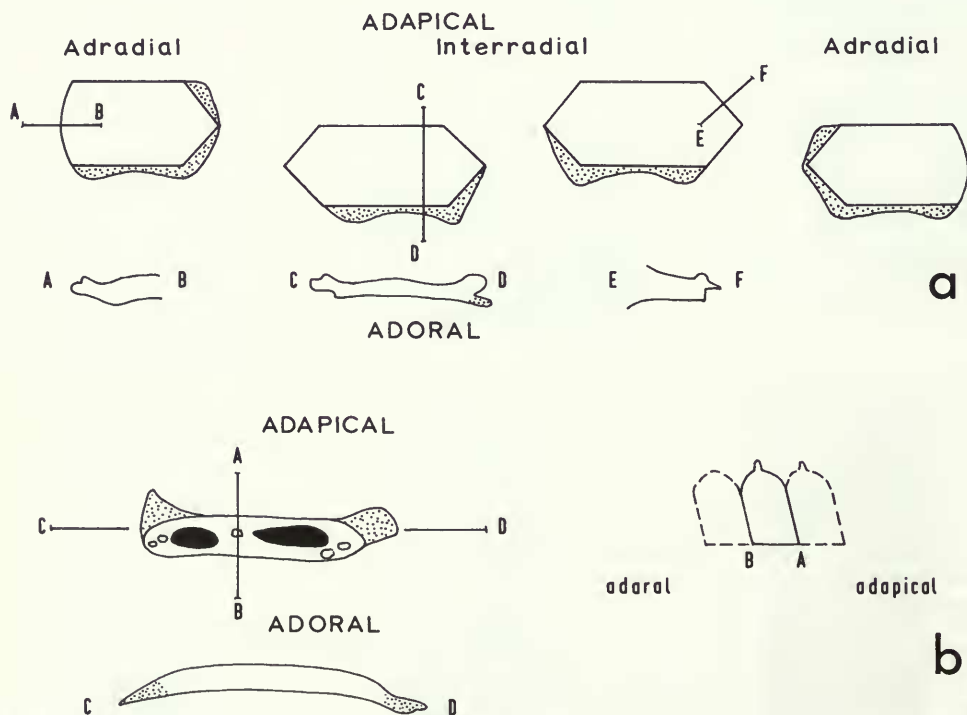

Fig. 20 Diagrams to show the positions of flanges (dotted) on (a) interambulacral and (b) ambulacral plates. Sketch sections show positions of flanges and facets.
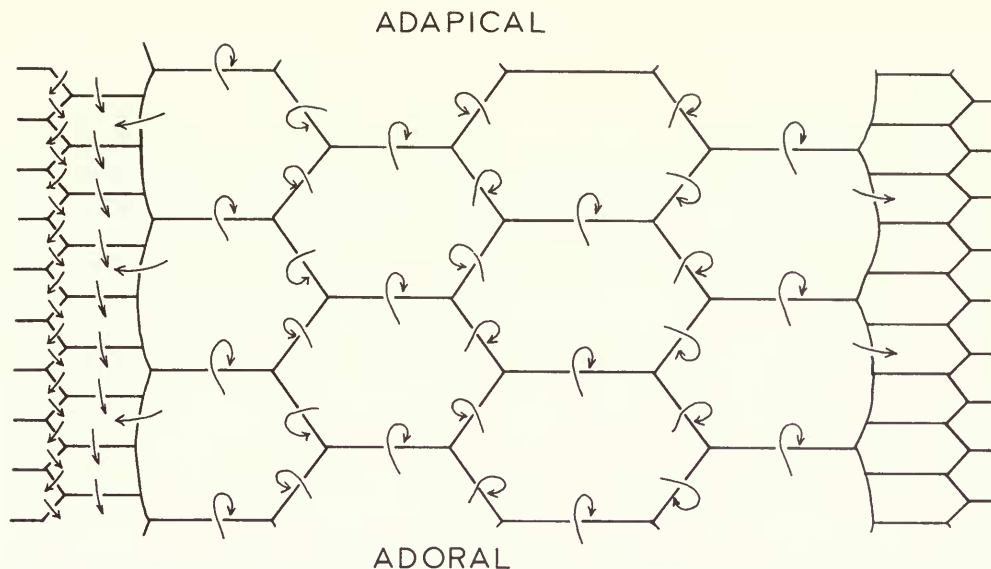
ADAPICAL

ADORAL

Fig. 21 Diagram to show directions of translation and directions of hinging when meridional muscle contracted. Gently curved arrows indicate direction of translation: reflexed arrows indicate direction of rotation.

of the radiole. The spinules may develop on opposite sides to each other, or they may develop alternately – there appears to be no constant pattern. Both arrangements do not, however, occur on the same radiole.

The shaft tapers towards the tip, and expands asymmetrically towards the milled ring, so that the shaft has its axis nearer to the adoral edge of the ring. The shaft has additional ornament of very fine longitudinal striations which increase in width over the collar before flaring out into the milled ring. The milled ring is tilted so that the adoral side is towards the tip of the shaft, and the adapical side is towards the tubercle. The striations forming the ridges of the milled ring continue to the underside, then stop at a raised rim. The rim is slightly concave where its adapical side joins the smooth base, and slightly convex on the adoral side. The deep acetabulum has a diameter about half that of the milled ring. It is centrally placed within the ring.

One of the primary radioles of the holotype is at least 51·5 mm long, but lacks the extreme tip. Some radioles have been crushed at the distal ends of their shafts in such a manner as to suggest hollow interiors. The paratype E.76889 has a few proximal ends of radioles remaining in contact with the test. These show hollow interiors near to the milled ring. Some radioles are slightly curved along their length, concave on their adapical sides. These are present mostly on the adapical surface of the holotype. The most adapical radioles are very much smaller than those at the ambitus.

(2) Secondary radioles (Figs 8, 13). These include the scrobicular radioles and the primary ambulacral radioles. All are small, about 6 mm long when complete, narrow, slender and solid. The shaft has ornament consisting of longitudinal striations somewhat coarser than the longitudinal striations of the primary interambulacral radioles. Each radiole has a thickening towards the proximal end which forms a milled ring. The base is smooth, convex and short, giving a bulbous appearance. The acetabulum is small.

The secondary radioles belong to the scrobicular tubercles, and to any other tubercles of this size and type which are not of the scrobicule. They are also attached to the tubercles of the ambulacra – the marginal tubercles and the tubercles of the adradial margins.

The secondary radioles of the holotype (see Figs 8, 13) are almost all present on the adapical surface of the test and the ambitus, but have been almost completely removed or

disrupted on the adoral surface. The radioles are almost *in situ* but have been laid flat upon the test. The secondary radioles of paratype E.76889 (Fig. 6) are close to their tubercles and occur in parallel bunches.

(3) Miliary radioles (Figs 13, 14b). These are very small – between about 1·8 mm and 3 mm long. In other respects they resemble the secondary radioles. Mostly they are preserved on the adapical surface of the holotype. They belong to the smallest tubercles to be found distributed randomly over the interambulacra, and also to the inner tubercles of the ambulacra. The miliary radioles of the ambulacra lie parallel to the perradial sutures on the holotype.

The secondary and miliary radioles are also present on paratype E.76887, where they have been scattered randomly over the test on both surfaces. Paratype E.76889 displays only primary and secondary radioles.

PEDICELLARIAE (Figs 13, 14a–b). There are two kinds of pedicellariae, both of them tridentate. The first is very large – almost as long as a secondary radiole, and the second kind is very small indeed, with valves barely as large as the 'bulb' of a secondary radiole. Both kinds are preserved only on the holotype.

The large pedicellariae (Fig. 14a) are present on the adapical and adoral side of the holotype, and on the adapical side are aligned parallel with the adjacent secondary radioles.

Each large pedicellaria consists of four parts – a stem and three valves. The stem is short, only about 2·8 mm long, and has a blunt proximal end, a cylindrical shaft and a short, tapered neck to join on to the proximal part of the valves. The valves each have a long, thin cylindrical part with longitudinal striations forming the ornament, and a triangular, rounded proximal part which is spoon-shaped and is about 0·5 m long, and has a dividing septum along the axis. The three valves fit together in a triple point which forms a flat surface for the stem to attach to. Where two valves are in contact at the proximal end there is a lens-shaped cavity. A complete valve is about 3·4 mm long. The complete pedicellaria is attached to a secondary tubercle. Some of the pedicellariae which are lying adjacent to secondary tubercles can be seen in interambulacra 2 and 3 of the holotype.

The smaller pedicellariae (Figs 13, 14b) are about 0·5 mm in total length; some are much smaller. They resemble the large pedicellariae in most respects except that the valves do not have the very long cylindrical distal part. Instead, the valves close a short way from the lens-shaped cavity. The stem joins a tubercle which is about a quarter of the size of a miliary tubercle. An example of a complete pedicellaria with its tubercle adjacent is present in interambulacrum 1. Others, with or without stems or tubercles, are present over the adapical face of the test, especially along the interambulacral margins of the adradial sutures.

COMPARISONS with other species of *Archaeocidaris*. *A. whatleyensis* differs from other species of the genus in that its primary radioles are approximately triangular in cross-section and bear only two rows of distally directed spinules. *A. triserrata* (American) and *A. triserialis* (European) are known only from their primary radioles which are triangular in section, but which have three rows of spinules. *A. triplex* (American) is known from primary radioles and some interambulacral plates. It has radioles with triangular cross-section and three rows of spinules. The plates are imperfectly known. Other species have different cross-sections and ornament on their radioles. These differences are summarized by Jackson (1912 : 258–259).

A. wervekei, from Germany and Belgium, differs from *A. whatleyensis* in that the height of its interambulacral plates equals or exceeds their width, and they have strong radial plications from basal terraces to plate margins. The interambulacral plates of *A. whatleyensis* on the other hand have greater width than height, and the radial plications of the tubercles are much less marked than those of *A. wervekei*.

A. urii, from Britain, Ireland, Belgium and Germany, is relatively common. It has many distally directed spinules on its radioles in many rows. The scrobicular tubercles are not so densely packed as those of *A. whatleyensis*, which also has many other secondary tubercles outside the scrobicular circles. *A. urii* does not have these tubercles. It has a smaller basal terrace and stronger radial plications to each tubercle than does *A. whatleyensis*.

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Fig. 22 Terminology of the margins and sutures of interambulacral and ambulacral plates.

A. nerei, from Belgium, has cylindrical radioles with very fine longitudinal striations. The interambulacral plates are more convex than those of *A. whatleyensis* and have far fewer secondary tubercles.

The known Aristotle's lanterns of *Archaeocidaris* are all very similar in appearance. They all have wide-angled pyramids with moderately deep foramina magna. Detailed information is mostly lacking. However, specimens of jaw fragments of *A. nerei* from the Tournaisian of Tournai, Belgium (see Jackson 1929) in the collections of the BM(NH) show similarities to the jaws of *A. whatleyensis*. The demipyramids of *A. nerei* have tuberculations on the pyramid–epiphyseal suture just as *A. whatleyensis* does. The arrangement is only slightly different, and this may be due to the much smaller size of the demipyramids of *A. nerei*, especially specimens from groups numbered 32846 and E.9328 in the BM(NH). The teeth of both species are serrated at their tips, but those of *A. nerei* are much more slender, and if the serrations were to be ignored the outline of the tips would be distinctly V-shaped and not semicircular as in *A. whatleyensis*. The median serration is raised above the lateral serrations and only overlaps the proximal end of one serration each side in *A. nerei*. Instead of a double-ridged central portion to each tooth, as in *A. whatleyensis*, there is a flattened V-shaped groove. Examples of these teeth have been examined in the BM(NH) from groups numbered E.9323 and E.9324.

Compasses are rarely found in Palaeozoic echinoids, but are previously known from *A. rossica*. The compasses of *A. rossica* do not have the very long prongs of the outer portion that are present in *A. whatleyensis*. Isolated outer portions of the compasses of undetermined Palaeozoic echinoids were reported by Hoare & Sturgeon (1976), and these also have short prongs. Hoare & Sturgeon also collected many isolated demipyramids which resemble those of *Archaeocidaris*, and which appear to have tuberculations on the upper surface where the epiphyses join, somewhat similar to those of *A. nerei* and *A. whatleyensis*. It is likely that other species of *Archaeocidaris* also have these tuberculations and pits, if only they could be found.

Discussion

The classification of the echinoids which is used by Fell (1966) in the *Treatise on*

Invertebrate Paleontology came before the rise of cladism. As a result the *Treatise* divides the Echinoidea into two groups – the Perischoechinoidea and the Euechinoidea. The Perischoechinoidea include all the Palaeozoic echinoids plus the Cidaroida, and the Euechinoidea includes all the remainder of the Echinoidea. In the light of Hennigian methodology this arrangement is unsatisfactory since, though the Euechinoidea are monophyletic, the Perischoechinoidea are paraphyletic (see Hennig 1969, 1981).

The basic concepts of Hennig no longer need explanation, but his ideas concerning the positioning of fossils in a classification are less well known. They depend on his concepts of the 'stem group' and what he called the '*group' (= crown group of Jefferies, 1979). These concepts are explained before we discuss how *Archaeocidaris* is related to other echinoids.

Suppose that two sister groups, 1 and 2, each contain several surviving member species. When fossils are considered, sister group 1 can be considered from two viewpoints.

The first is a narrower viewpoint comprising the latest common ancestral species of living members of group 1 and all descendants of that species living or extinct. This is the *crown group*. The second is a wider viewpoint comprising all descendants of the latest common ancestor of both groups 1 and 2, but minus all members of group 2. The wider viewpoint is the *total group* 1. If the crown group of group 1 is removed from total group 1 the remaining forms are called the *stem group* of group 1. The stem group is composed of extinct forms and is paraphyletic. It includes those species leading from the latest common ancestor of both groups 1 and 2 to the latest common ancestor of group 1 (the *stem line*) and also all descendants of that line except members of the crown group.

All surviving monophyletic groups with more than one species can be divided into stem groups and crown groups, but this is only useful if fossils are known. The real advantage of the stem group concept is that fossil species can be assigned to a stem group merely by the presence or absence of synapomorphies. To *prove* that a fossil belongs to a stem line of descent, on the other hand, requires complete stratigraphical data for all the species involved.

The stem group can be divided further by noting how closely related its component species are to the members of the crown group. The synapomorphies characterizing a member of an extant monophyletic group have not evolved all at once but by stages, being present in some members of the stem group and primitively absent in others. This enables the stem group to be split into *intermediate categories* (*Zwischenkategorien* of Hennig). The smallest unit of an intermediate category is the *plesion* (Patterson & Rosen 1977), which comprises all those members of a stem group which are equally related to the crown group. The plesion will possess a synapomorphy in common with the crown group which more primitive plesions lack, and will lack a synapomorphy which more advanced plesions have. This is sometimes confused by a character being secondarily lost.

The classification of the echinoids can be expressed in terms of sister groups and of stem and crown groups, and a cladogram constructed (Fig. 23). This shows that the presumed ancestor had the following characters: four or more columns of plates per interambulacrum; a flexible test; hollow primary interambulacral radioles; perforate primary interambulacral tubercles; a hinge-jointed lantern; shallow-angled pyramids; a fairly deep, U-shaped foramen magnum; a pyramid–epiphyseal suture with pits and tuberculations; and peristomial plates with two columns per ambulacrum and many columns of interradial plates.

The synapomorphies of stem and crown echinoids are as follows (numbers refer to Fig. 23):

1. Gain of triangular section for primary interambulacral radioles.
2. Gain of rigid interambulacra.
3. Gain of rigid test.
4. Gain of solid radioles.
5. Gain of apophyses in perignathic girdle.
6. Gain of steep-angled pyramids.
7. Gain of crenulate tubercles.
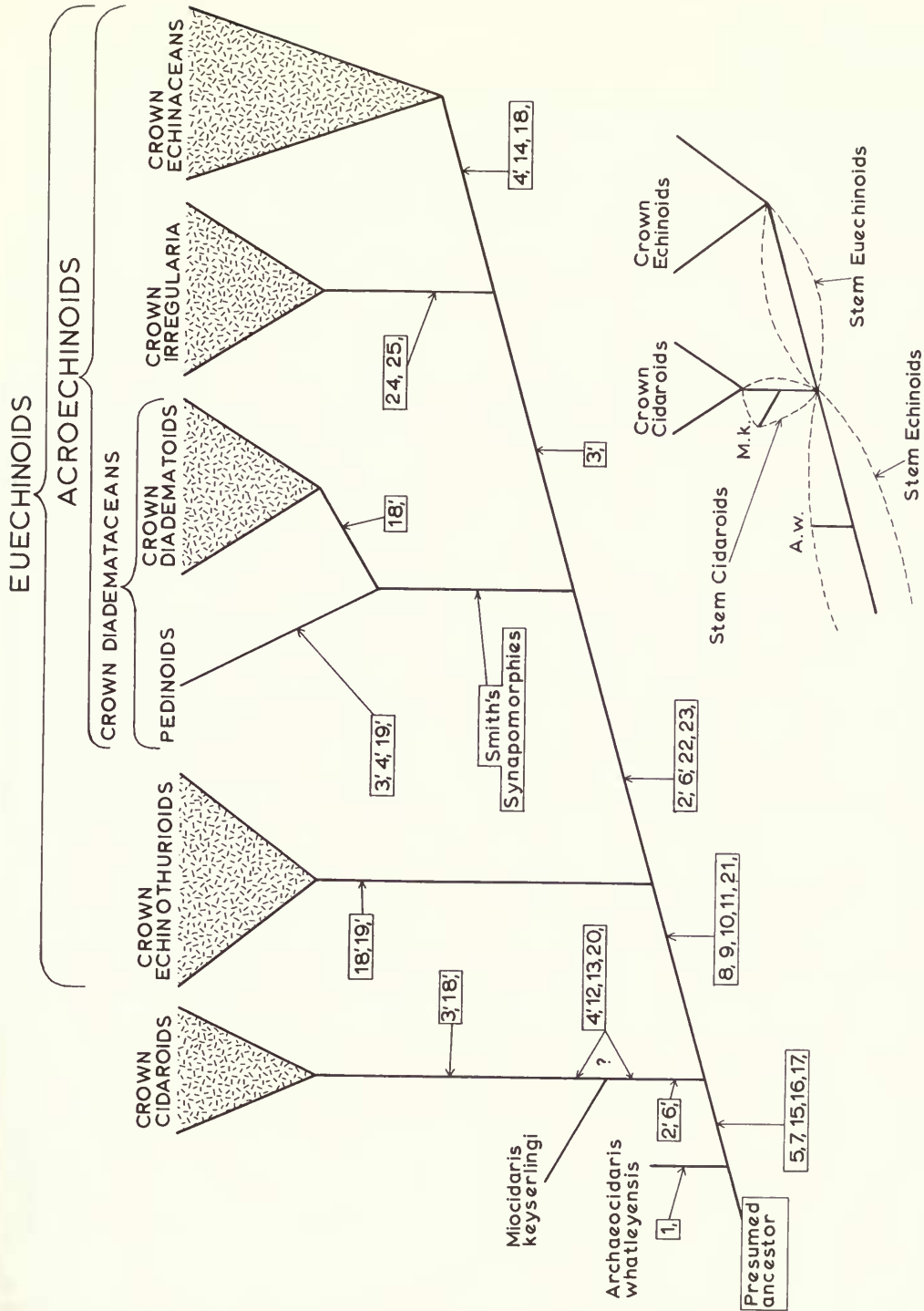8. Gain of smooth-surfaced pyramid–epiphyseal sutures with deep pits in demipyramids.

Fig. 23 Cladogram showing the principal synapomorphies of the stem echinoids, the cidaroids and the euechinoids; see text for detailed explanation. When a feature evolves more than once we have inserted a '', e.g. 3', whenever it appears.

9. Gain of auricles.
10. Gain of external gills and gill slits.
11. Gain of compound ambulacral plates.
12. Gain of socket-joint lantern.
13. Gain of shallow foramen magnum.
14. Gain of keeled teeth.
15. Loss of two columns of plates per interambulacrum.
16. Loss of tuberculation of pyramid–epiphyseal suture.
17. Loss of all interradial buccal plates except for one column.
18. Loss of flanges on plates.
19. Loss of crenulations on tubercles.
20. Loss of pits in pyramid–epiphyseal suture.
21. Loss of interradial buccal plates.
22. Loss of ambulacral buccal plates except five pairs at the mouth.
23. Loss of Stewart's organs.
24. Loss of periproct from apical disc by migration adorally.
25. Gain of bilateral symmetry.

The cladogram shows the Archaeocidaridae as part of the stem group of the Echinoidea. *Miocidaris keyserlingi* belongs to the stem group of the cidaroids. The echinothurioids are the primitive sister group to the acroechinoids, i.e. all the remaining euechinoids (see Smith 1981). The diademataceans (*sensu* Smith, 1981) comprise the pedinoids plus the diadematoids, with the pedinoids as the sister group to the diadematoids. The echinaceans include all the remaining echinoids except the Irregularia (*sensu* Smith, 1981). The echinothurioids plus acroechinoids make up the crown Euechinoidea. The *Treatise* taxon Perischoechinoidea, which groups together all Palaeozoic echinoids plus the Cidaroida, must be rejected because it is paraphyletic and is not a stem group.

The cladogram suggests that the presumed ancestor in Fig. 23 had features which are still represented in living euechinoids. But *Archaeocidaris* possesses at least one character more primitive than any possessed by crown echinoids, i.e. four columns of plates per interambulacrum. It also possesses features which were probably shared with the latest common ancestor of living echinoids, i.e. the first crown echinoid. These features include: a flexible test, perhaps hollow primary radioles, hinge joints in the lantern, shallow-angled pyramids, fairly deep, U-shaped foramina magna, pyramid–epiphyseal suture with pits and tuberculations, perforate tubercles, and many rows of buccal plates both ambulacral and interradial. Descendants of the first crown echinoids may retain some of these primitive characters, but have lost others.

Sarasin & Sarasin (1887–8), in their description of the living echinothurioid *Phormosoma*, described the method by which the ambulacral plates imbricate over each other. This happens by means of the meridionial muscles which are attached to the aboral parts of the auricles at one end and to the ocular plates at the other, and pass along the inner adradial edge of the ambulacral plates, and also the peristomial plates. By contracting these muscles, the ambulacra are shortened, causing the ambulacral plates to imbricate adorally, and at the same time increasing the curvature of the test by causing the interambulacra to bend at the plate margins. It seems likely that similar muscles were present along the corresponding ambulacral margins of *Archaeocidaris*, with comparable effects when they contracted. However, the meridional muscles were not found in diadematids when these were examined by the Sarasins. At the adradial margins of *Archaeocidaris* the interambulacra imbricated perradially over the ambulacra. The mesenteries of living diadematids, though apparently without muscles, are arranged exactly like the muscle-bearing mesenteries of *Phormosoma*, which suggests that such arrangement of mesenteries is primitive for crown euechinoids and could well have existed in *Archaeocidaris* also.

Flexible tests were present in stem echinoids such as the Archaeocidarids, stem cidaroids and in primitive crown echinoids. Some species placed traditionally in the genus *Miocidaris* had tests which were either wholly flexible or only partly so. Those which had wholly flexible tests have ambulacral plates of a similar construction to those of *Archaeocidaris*

(Kier 1965, 1968). They are very like an *Archaeocidaris* but with only two columns of plates per interambulacrum (e.g. *Miocidaris connorsi* Kier, 1965). The species of *Miocidaris* with entirely flexible tests are either advanced stem echinoids, or are primitive stem euechinoids or stem cidaroids. The species with rigid interambulacra such as *M. keyserlingi* are probably stem cidaroids. Crown cidaroids have rigid tests. *Miocidaris* as defined in the *Treatise* is paraphyletic.

Some living euechinoids have flexible tests. Echinothurioids such as *Phormosoma* are wholly flexible by means of a tough flexible membrane between the plates which allows flexing of the test and holds the plates together. There are no flanges on its interambulacral plates. If the flexibility of the tests of echinothurioids is homologous with that of *Archaeocidaris*, they form the primitive sister group to all other living euechinoids. These others have been called the Acroechinoidea by Smith (1981) and their tests are more rigid than those of echinothurioids, though diadematoids retain slight flexibility. The rigid test of acroechinoids was probably acquired independently of that of cidaroids.

Stem echinoids such as *Archaeocidaris* did not possess a perignathic girdle for the attachment of the lantern muscles. These muscles were presumably attached directly to the interambulacral plates of the peristome. Stem cidaroids, however, had a perignathic girdle, formed by the apophyses. Crown euechinoids have apophyses and auricles. Stem echinoids and all cidaroids have no gill slits, but these are present in the euechinoids.

Peristomial plates extend from the border of the peristome to the mouth and may consist of ambulacral plates, interradial plates, and in some euechinoids some plates of uncertain origin. In *Archaeocidaris* the plates of the peristome consist of several columns of imbricating perforate ambulacral plates, and several columns of imbricating interradial plates. This is probably the case for all stem echinoids. Stem and crown cidaroids have two columns of ambulacral peristomial plates extending from each ambulacrum to the mouth. There is only one column of interradial plates extending from the peristomial border to the mouth of crown cidaroids; the evidence for interradial plates in stem cidaroids is lacking. The echinothurioid *Phormosoma* has two columns of large ambulacral peristomial plates extending from each ambulacrum, but it has no interradial plates. A syntype of the type species of *Echinothuria* (BM(NH) 40240)) has part of a double column of ambulacral peristomial plates preserved, but has no interradial plates visible. It is most likely that *Echinothuria* resembled *Phormosoma* in this respect. The diademataceans, as part of the advanced sister group to the echinothurioids, have only five pairs of peristomial plates in a ring around the mouth. Thus, the primitive condition of the peristomial plating seems to be that of many columns of ambulacral and interradial plates as found in *Archaeocidaris*. From this came the double columns of ambulacral plates plus single rows of interradial plates as in the cidaroids, and the double columns of ambulacral plates only, as in *Phormosoma*. From a *Phormosoma*-like condition arose the situation with just five pairs of ambulacral oral plates situated at the edge of the mouth, as in *Diadema*.

Some features of the Aristotle's lantern have also evolved. The pyramids of *Archaeocidaris* are low-angled and wide, each with a fairly deep and broad foramen magnum. The demipyramid–epiphyseal suture is very tuberculate, with shallow pits in the upper surface of the demipyramid. Crown cidaroids have steep-angled pyramids, each with a very shallow foramen magnum, and smooth demipyramid–epiphyseal sutures with no tuberculations or pits. *Echinothuria* has pyramids which are steeper-angled, but its living relative *Phormosoma* has shallow-angled pyramids reminiscent of *Archaeocidaris*. However, *Phormosoma* does not have the complex tuberculation and shallow pits on the demipyramid–epiphyseal suture. Instead these surfaces are smooth, with deep pits in the demipyramid. If the shallow pits of *Archaeocidaris* are homologous with the deep pits in the demipyramids of the crown euechinoids, then this feature will be a primitive character as compared with the smooth surface without pits of the cidaroids. The fairly deep U-shaped foramen magnum of *Archaeocidaris* is primitive when compared with the shallow foramen magnum of cidaroids, and the deep V-shaped foramen magnum of the euechinoids.

Märkel (1979) described the two different types of joint between the epiphyses and the rotulae in living cidaroids and non-cidaroids. He calls the joints 'socket joints' in the cidaroids, using *Eucidaris tribuloides* as an example, and 'hinge joints' in non-cidaroids. Cidaroids have hemispherical condyles on the rotulae, with corresponding hemispherical glenoid cavities in the epiphyses to form ball-and-socket joints. The non-cidaroid joints have elongate condyles and glenoid cavities to form a hinge. *Archaeocidaris*, however, has the hinge-joint type, unlike living cidaroids and exactly like living euechinoids. The hinge joint is therefore probably a primitive character already present in the stem echinoids, present in the first crown echinoid and retained in living non-cidaroids, whereas the socket joint is an advanced cidaroid character.

The primary radioles of *A. whatleyensis*, some other species of *Archaeocidaris*, echinothurioids, diadematoids, early pedinoids (*sensu* Smith, 1981), atelostomes and gnathostomes are hollow for all or most of their lengths. Other species of *Archaeocidaris*, *Miocidaris*, crown cidaroids and remaining acroechinoids have solid primary radioles. If hollow radioles are a primitive character then *Archaeocidaris* contains two groups. The group with hollow radioles would be closer to the primitive condition and would be paraphyletic, whilst the group with solid radioles is probably a monophyletic group showing parallelism with the cidaroids and also some acroechinoids. If the radioles of *M. connorsi* are hollow, as suggested by the photograph in Kier (1965), this supports the idea that hollow radioles are primitive for crown echinoids.

The ambulacral plates of *Archaeocidaris* and *Miocidaris* are not compound but form two simple columns in each ambulacrum. Some crown cidaroids show a simple kind of compounding (probably better called pseudocompounding), e.g. *Stereocidaris grandis*, *Paracidaris*, *Diplocidaris*, *Alpicidaris* and *Tetracidaris* (see Mortensen 1928 : 11–15). In these genera the marginal tubercle of one plate increases in size so that it sometimes displaces the marginal tubercle of adjacent plates, and sometimes the adjacent plates lack the tubercle. The enlarged tubercle only develops on its own plate. In *Diplocidaris* the pores are displaced alternately to give a double series of pore-pairs. This kind of compounding is probably a parallelism with that of the euechinoids. Diadematids have plate compounding in their typical triads, and *Echinothuria* and *Phormosoma* have a version of diadematid triad compounding sometimes similar to the 'arbacioid' type of compounding (see *Treatise*; Fell 1966 : 231).

The primary interambulacral tubercles of *Archaeocidaris* and the echinothurioids are perforate and non-crenulate, whilst those of *Miocidaris* (e.g. *M. keyserlingi*) are perforate and crenulate. Crown cidaroids may or may not have crenulate tubercles, but all have perforate tubercles except the Psychocidaridae (e.g. *Tylocidaris*) which have non-perforate tubercles. *Tylocidaris* bears traces of perforation in the most adapical interambulacral tubercles, indicating that loss of perforation in this genus is secondary. Diadematids have perforate tubercles and may or may not have crenulate tubercles.

Within the *Treatise* definition of the Miocidaridae there are some genera which have crenulate primary interambulacral tubercles, and others with non-crenulate tubercles. Crown cidaroids have genera with either crenulate or non-crenulate tubercles. The primitive condition for crown cidaroids was almost certainly with crenulate tubercles as in the stem cidaroid *M. keyserlingi*. On the other hand, the absence of crenulations in *Archaeocidaris* (and all other Palaeozoic echinoids) is most likely to be primitive. Either crenulations are primitive for crown echinoids, or they have evolved more than once. If they have evolved more than once then miocidarids with crenulate tubercles are probably stem cidaroids, and the crenulate tubercles of some acroechinoids evolved separately. If they have evolved once only and have been lost several times then 'miocidarids' with crenulate tubercles could be advanced stem echinoids, with some crown cidaroids, echinothurioids, and some euechinoids losing their crenulations. It is more parsimonious to suppose that crenulate tubercles evolved once and have been lost several times than to believe they evolved more than once.

Conclusions

A. whatleyensis, and *Archaeocidaris* in general, is shown to be a stem echinoid by the presence of four columns of plates in each interambulacrum. *A. whatleyensis* demonstrates that many features which have been seen as synapomorphies of euechinoids in fact existed already in the stem group of echinoids. These features of the euechinoids may therefore be considered to be probably primitive for crown echinoids as a whole. They include:

1. Upper surface of pyramids with pits.
2. Hinge joints in the Aristotle's lantern.
3. Shallow pyramid angles in the lantern, with broad, U-shaped foramina magna.
4. Perhaps hollow radioles.

Moreover, the flexibility of the test of *Archaeocidaris* is probably homologous with that of echinothurioids. The rigid test of acroechinoids has therefore probably been acquired independently of that of the cidaroids.

Crown cidaroids have some advanced characters which are unique to them, and which are represented in the euechinoids by more primitive characters. The advanced characters include:

1. Upper surface of pyramids smooth, without pits.
2. Socket joints in the lantern.
3. Shallow and small foramina magna, steep pyramid angles.

The rigid test of crown cidaroids has probably been acquired separately from that of the acroechinoids.

Acknowledgements

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